THE ARISTIDA CALIFORNICA-GLABRATA COMPLEX (GRAMINEAE)

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ABSTRACT

Two closely related taxa of the Aristida californica complex differ primarily in having either pubescent or glabrous culms. The pubescent form, A. californica, was described by Thurber in 1880. Eleven years later plants with glabrous culms were named A. californica var. glabrata by Vasey. Hitchcock elevated Vasey's variety to species rank in 1924, a disposition which has been accepted generally by subsequent botanists.

To determine whether these taxa merit specific rank, collections from throughout the ranges of both were analyzed utilizing five spikelet characters. Measurements of length of both glumes, lemma, awn column, and free awns revealed a high degree of overlap; for the lemma, the overlap was complete. Chromosome counts (2n=22) are reported for the first time for collections of both taxa. Even though their geographical ranges are reasonably separate, and they tend to occur at different elevations, we conclude that it is more realistic to treat them as varieties of a single species.

RESUMEN

Dos taxa cercanas, pertenecientes al complejo de *Aristida californica*, difieren principalmente en la superficie del culmo; una es pubescente y la otra es glabra. La forma pubescente, *A. californica*, fué descrita por Thurber en 1880. Once años después, plantas con culmos glabros fueron llamadas *A. californica* var. *glabrata* por Vasey. La última taxon fué elevada al nivel de especie por Hitchcock en 1924.

Para determinar la categoria más correcta, hemos analizada colecciones de la distribución entera para ambas taxa, con la base de cinco caracteres de la espiguilla. Las medidas de longitud de ambas glumas, la lemma, la columna de las aristas, y las aristas libres, revelaron un alto grado de traslapo; para la lemma esté fué completo. Se reporta por primera vez el número cromosómico (2n=22) para las ambas taxa. Aunque sus distribuciones geográficas están separadas razonablemente y, en general, ellas tienden a ocupar altitudes diferentes, es nuestra opinión que una mejor taxonomia resulta cuando éstas taxa estan consideradas como dos variedades de una sola especie.

Aristida californica was described by Thurber (1880), who cited collections from the Colorado Desert (Schott) and Fort Mohave (Cooper). There is no problem regarding the identity of the plant, which is described as being tufted, the culms pubescent, branched above, and with the awn column articulated with the lemma body,

from which it separates at maturity. Thurber stated: "It is the only species of the section with articulated, caducous awns (*Arthratherum*) thus far found in North America." This comment is not strictly correct, but Thurber can be forgiven. Although two other North American species, *A. tuberculosa* Nutt. (1818) and *A. desmantha* Trin. & Rupr. (1842), have the characteristics of the section, this fact had not been recognized when Thurber described *A. californica* in 1880.

The section Arthratherum was established by Reichenbach (1828), based on the genus Arthratherum P. Beauv. (1812). Neither Reichenbach nor Trinius and Ruprecht (1842), who monographed the genus, had recognized either A. tuberculosa or A. desmantha as belonging to the section. Moreover, Trinius and Ruprecht indicated that members of the section Arthratherum are confined to Africa, Asia, and Australia. In that work we find A. tuberculosa and A. desmantha listed under "§.I. Aristida (genuina)." [=Sect. Aristida].

Hitchcock (1924) seems to have chosen the Cooper specimen as "lectotype," indicating that it is in the U.S. National Herbarium. Among the specimens he cites, one finds: Fort Mohave, Cooper 2217. Moreover, Henrard (1926) states that a fragment of the specimen collected by Dr. Cooper "was kindly received from Prof. Hitchcock." An illustration of Aristida californica in Henrard's revision (p. 66) bears the caption: "From cotype (Fort Mohave, Dr. Cooper 2217)." Neither Hitchcock nor Henrard mentions having examined a Schott collection. Although Hitchcock did not specifically state he was choosing the Cooper specimen as lectotype, it is clear that he considered it to be "type material." To prevent any future ambiguity regarding the type of this species, we here designate Cooper 2217 (US-81008) as lectotype of Aristida californica Thurber.

Ten years after the publication of *Aristida californica*, Vasey (1891) described a form with glabrous culms, giving it the name var. *glabrata*. It was based on a collection made by T. S. Brandegee at San José del Cabo, Baja California Sur, Mexico, in 1890. Vasey noted that along with the glabrous culms, this taxon differs from the type [A. californica] in its larger size, more spreading and branching habit and shorter-awned flowering glumes [lemmas], yet appears to be too near for a new species.

In his revision of *Aristida*, Hitchcock (1924) elevated Vasey's var. *glabrata* to the rank of species. He gave a complete description of the taxon, and noted that it differs from *A. californica* in the glabrous culms, shorter awn column, and longer, more densely flowered panicles. This transfer has been accepted, without comment, by all subsequent botanists. The key character has been pubescent versus glabrous culms, although differences in glume and awn column length are frequently mentioned.

In the same publication, Hitchcock (1924) described a third mem-

ber of Sect. Arthratherum, A. peninsularis, based on Palmer 501 collected in Nov 1887 at Bahía de Los Angeles, Baja California Norte, Mexico. It was said to have pubescent culms like A. californica, but to differ in being annual, and having larger glumes, lemmas, and awns. Henrard (1926) accepted this species without expressed reservations, as have most other botanists. The sole exception is Gould and Moran (1981), who treat it as a synonym of A. californica. They comment that since no distinctly annual plants have been found (in the type locality), A. peninsularis must be only an annual appearing form of A. californica. We quite agree with this conclusion; all plants of this complex, from any area, are apparently perennial, although they may flower during their first year of growth. Regarding Hitchcock's statement that the spikelet parts are larger in his A. peninsularis, with the exception of the lemma (which he gives as "about 8 mm"), we found his measurements fall well within the range we determined for A. californica. We examined several specimens from the type locality and none had lemmas longer than 7 mm. We did not see the type.

The present study addresses the question of whether or not the two taxa, Aristida californica and A. glabrata, are sufficiently distinct to merit specific designation. Vegetatively, the plants exhibit no important differences except for the culms, which are completely glabrous or variously pubescent. The indument, when present, may be rather long and somewhat matted, or extremely short. Various gradations between these two extremes are encountered when a large suite of specimens is examined. Some culms which are devoid of hair may be quite scabrous and, therefore differ but slightly in appearance from others with very short hairs. Nevertheless, one experiences little difficulty in scoring plants as either "glabrous" or "pubescent," and this reasonably consistent feature has been the key character used to separate the two taxa. The basis for naming herbarium specimens also, obviously has been this one feature, and little importance seems to have been placed on whether the hairs are long or short. Along with the pubescent or glabrous culms, authors frequently indicate slight differences in lengths of glumes, and especially the awn column, and free awns. Thus Hitchcock (1951) states that the awn column in A. californica is 15 to 20 mm long in contrast to that in A. glabrata which he indicates is 6 to 14 mm. In Gould and Moran (1981) the awn length in A. californica is said to be 2.5 to 4.5 cm versus 1.5 to 4 cm in A. glabrata.

METHODS

At ARIZ there is a rather large collection representing this complex, which includes gatherings made by both authors over a period of years. In addition, specimens were borrowed from ASU, CAS-

DS, RSA-POM, SD, and UC-JEPS. Our sample consisted of 145 plants with some pubescence on the culms, and 84 in which the culms were completely glabrous. Because plants of the two taxa are very similar vegetatively, we focused on the spikelet: glumes, lemma, awn column, and free awns. To determine the amount of variability in size of spikelet parts on a single individual, we measured ten spikelets on each of four specimens—two with pubescent culms and two with glabrous culms. Care was taken to select spikelets which we judged to be mature, as evidenced by fully developed caryopses within the lemma. Summary statistics were calculated for the 229 specimens, using mean, standard deviation, standard error of the mean, and skewness. Some field work was carried out especially for this study, primarily to gain more information on range and to collect cytological material.

RESULTS

Among the specimens borrowed from UC-JEPS we found two types. One of these was *Cooper s.n.* collected at Fort Mohave in 1860-61 (UC-37301). This is one of the two collections cited by Thurber in his original description of *Aristida californica* and is thus a syntype; the specimen at US was designated as lectotype earlier in this paper. UC-37301 is, therefore, an isolectotype of *A. californica* Thurb. This specimen has moderately "woolly" culms, but the hairs are not as dense and long as in many other examples of this species. The first glume measures 7–9 mm, the second ca. 15. The lemma is 6.5–7 mm, with a column 14–15 mm, and the awns are 3–4 cm in length.

An apparent isotype of *Aristida californica* var. *glabrata* Vasey is UC-121421. This specimen was collected by T. S. Brandegee (s.n.) at San José del Cabo, Baja Californica Sur, Mexico, 1 Oct 1890. [The Chase Index cites this collection as *Brandegee 34*.] The culms of the UC plant are completely glabrous. The first glume measures 5 mm in length; the second ca. 10 mm. The lemma is 6–6.5 mm, with a column ca. 8 mm, and awns only ca. 2 cm. Clearly, plants representing the types of these two taxa exhibit other differences besides pubescent versus glabrous culms. In var. *glabrata* the glumes are somewhat shorter, and this is also true for the awn column and the spreading awns.

Table 1 summarizes the results obtained from measuring spikelet parts on a single individual; Table 2 presents the data from all specimens studied, and this information is also shown in graphic form in Figure 1.

CHROMOSOMES

Since we found no published chromosome numbers for members of this complex, along with collecting herbarium specimens, one of

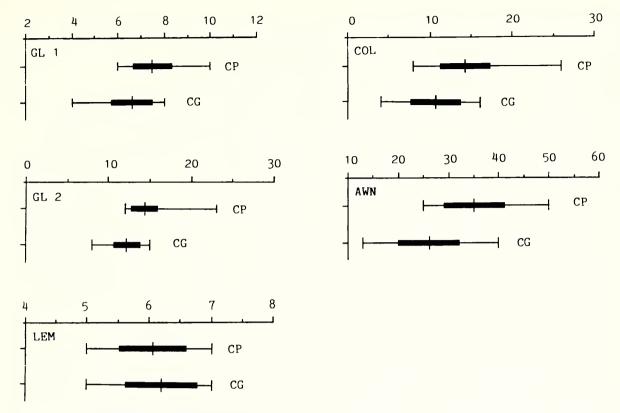


FIG. 1. Summary of measurements in mm of glume 1, glume 2, lemma, awn column, and free awn for the two taxa of the *Aristida californica* complex. Plants with pubescent culms (CP); those with glabrous culms (CG). The diagrams illustrate the range, mean, and the mean \pm 1 standard deviation.

us (Reeder) preserved young inflorescences in the standard 3:1 absolute alcohol-acetic acid mixture for cytological examination. The anthers were later squashed in aceto-carmine. Whether or not the plants had pubescent or glabrous culms, all were determined to be diploid (2n=22). The collections are listed below. Collection numbers are those of John R. and Charlotte G. Reeder. Vouchers are at ARIZ.

Aristida californica Thurb. var. californica: USA. AZ: Pima Co., Cabeza Prieta Natl. Wildlife Refuge, 180 m, 5 Mar 1977, 6835; CA: Imperial Co., 20 km W of Glamis along CA-78, sea level, 1 Oct 1987, 8160.

Table 1. Summary of Ten Measurements for Each of Five Spikelet Characters on Four Different Specimens of the *Aristida Californica* Complex. Measurements in mm. All specimens are at ARIZ.

	Culms p	oubescent	Culms glabrous		
	Reeder 8238	Felger 16712	Reeder 7221	Wiggins 7239	
	AZ, YUMA	MEX, SON	MEX, BCN	MEX, SON	
1st glume	7.0–8.5	6.5–8.0	5.5–8.0	7.0–9.2	
2nd glume	14.0–16.0	13.0–15.0	11.5–13.5	13.0–13.5	
Lemma Awn column	6.0–6.5	5.0–6.0	5.0–6.3	6.2–7.0	
	11.5–16.0	12.0–18.0	12.0–16.0	12.0–16.0	
Free awn	35.0–40.0	40.0–45.0	22.0–27.0	32.0–38.0	

Table 2. Summary Statistics for the Five Key Characters of the Aristida Californica Complex. Plants with pubescent culms (CP), n = 145; those with glabrous culms (CG), n = 84. Measurements in mm.

Character	Taxon	Mean	SD	SE	Min.	Max.	Skewness
1st glume	СР	7.50	0.835	0.069	6.0	10.0	0.466
	CG	6.63	0.912	0.100	4.0	9.2	-0.348
2nd glume	CP	14.34	1.506	0.125	12.0	23.0	1.814
C	CG	12.24	1.402	0.153	8.0	15.0	-0.298
Lemma	CP	6.06	0.537	0.045	5.0	7.0	0.016
	CG	6.20	0.567	0.063	5.0	7.0	-0.284
Awn Col.	CP	14.31	3.250	0.270	8.0	26.0	0.768
	CG	10.60	2.760	0.301	4.0	16.0	-0.138
Awn (free)	CP	35.12	5.644	0.469	25.0	50.0	0.058
	CG	26.07	6.211	0.678	13.0	40.0	-0.304

Aristida californica Thurb. var. glabrata Vasey: USA. AZ: Cochise Co., on Willcox Rd. just E of jct. with Cascabel Rd., 975 m, 5 Jun 1987, 8041; Pima Co., Santa Rita Range Reserve along Box Canyon Rd., 1310 m, 29 May 1987, 8035; E end of Rincon Mts, 1220 m, 4 Jun 1987, 8038; Pinal Co., Pinal Pioneer Pkwy., 3 km S of Bradley Wash, 1310 m, 3 Oct 1986, 7994; Yavapai Co., along US-93, 3.5 km NW of Santa Maria River crossing, 550 m, 2 Oct 1987, 8162; along US-93, ca. 4.5 km NW of jct. with US-89, 670 m, 2 Oct 1987, 8163.

DISCUSSION

Table 1 needs little explanation. It reveals, as we suspected, that there is a considerable amount of variation in lengths of spikelet parts on a single individual. This was taken into consideration as measurements were made on the entire suite of specimens examined in the study. For each sample numerous spikelets were measured in order to arrive at a value which seemed representative.

Perusal of Table 2 reveals that in each case there is a considerable amount of overlap in the measurements of the spikelet parts; with the lemma, this overlap is complete. With respect to glume I, we determined that 89% of CP and 88% of CG plants fell in the zone of overlap, which is 6–8 mm. Glume II had 99% of CP and 77% of CG plants in the overlap zone of 12–18 mm. The awn column showed 79% of CP and 88% of CG plants in the overlap zone of 8–16 mm. Finally, the spreading awns, with an overlap zone of 25–40 mm, revealed a similar picture: 90% of CP and 65% of CG plants fell in this zone. It is evident that lengths of these spikelet features are not good key characters to use in separating species. For each feature (except the lemma) the longest measurement is from a plant

with pubescent culms, whereas the shortest is from one in which the culms are glabrous.

ECOLOGY AND GEOGRAPHICAL DISTRIBUTION

The pubescent taxon occurs in southeastern California, Baja California Norte and Sur, southwestern Arizona, and in Sonora southward along coastal dunes to Bahía Colorado (south of Tastiota) and farther south from near the mouth of the Río Mayo to Topolobampo in northwestern Sinaloa (Fig. 2). This is one of the few grasses reported to be endemic to the Sonoran Desert, but, as the collections from Sinaloa indicate, it actually occurs south of the Sonoran Desert. It is also in the Mojave Desert of California.

Densely pubescent populations inhabit sandy soils, flats and dunes, in the lowland regions of the northern part of the Sonoran Desert of northwestern Sonora, extreme southwestern Arizona, southeastern California, and northeastern Baja California Norte. This area was designated by Shreve (1951) as the Lower Colorado Valley phytogeographic region of the Sonoran Desert. Here rainfall is largely winter-spring, almost entirely so in the western part, and this is also true for the Mojave Desert of southern California. There may be some summer rainfall in the more southern and eastern portion of the Lower Colorado Valley, although precipitation in this extremely arid region is unpredictable (Ezcurra and Rodriguez 1986).

The pubescent form also occurs southward into regions of relatively greater and more predictable rainfall in the Baja California peninsula and in southern Sonora and northwestern Sinaloa considerably south of Guaymas, the usually accepted boundary of the Sonoran Desert (Felger and Lowe 1976). The southern Sonora and Sinaloa populations are disjuncts, presently known from coastal dunes in the delta regions of the Río Mayo and Río Fuerte (we predict that it should also occur in coastal dunes in the delta region of the Río Yaqui). Plants from these southern populations are not as densely pubescent as are those from the Lower Colorado Valley and Mojave Desert.

Aristida glabrata generally occupies regions peripheral to that of A. californica, in areas of higher elevation (Fig. 3) and/or higher precipitation, and mostly where summer-fall rainfall is greater and more predictable. In Arizona and Sonora A. glabrata extends into grassland and chaparral well above the desert. In addition, this species often occurs on soils which are more rocky and gravelly than those occupied by A. californica. Throughout their distribution the two taxa are essentially allopatric, but in a few cases they have been collected in close proximity. Both have been found in Baja California Norte, in the San Matías Pass, at only slightly different elevations [Reeder and Reeder 7221, 700 m, A. glabrata (ARIZ); and Thorne

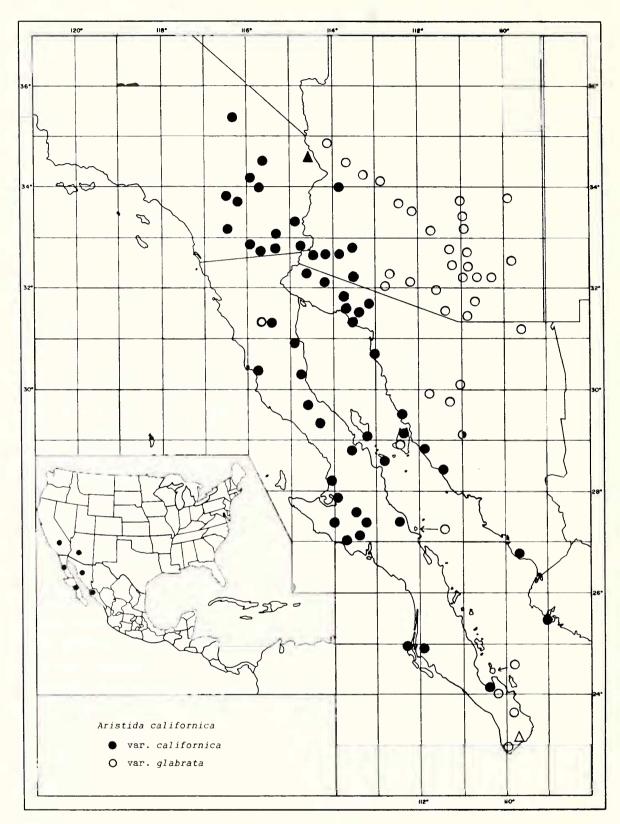


Fig. 2. Map showing the range for the two varieties of *Aristida californica*: var. *californica* (solid circles); var. *glabrata* (open circles). Triangles represent type localities.

and Charlton 60184, 600 m, A. californica (RSA)]. Another somewhat similar situation is encountered in the vicinity of La Paz, Baja California Sur. There are several collections of A. glabrata from that region, and we have seen one gathering of A. californica from this

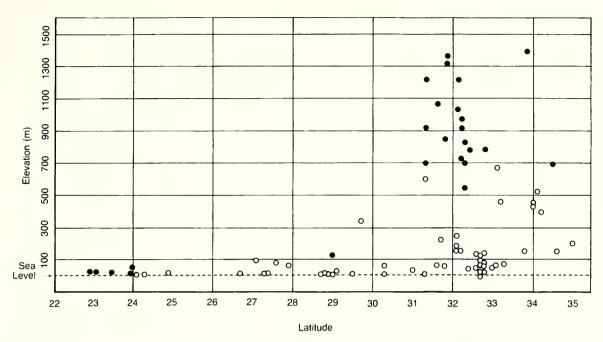


Fig. 3. Elevational distribution for *Aristida californica* var. *californica* (solid circles) and var. *glabrata* (open circles).

same area [Carter 2726 (UC)]. Both taxa have also been found on Tiburón Island in the Gulf of California. Aristida californica [Felger and Russell 7009; Felger et al. 12537 (ARIZ)] is common on the beach dunes of the arid eastern and northern coasts (Felger and Lowe 1976); one collection of A. glabrata [Felger et al. 17351 (ARIZ)] was made from the large interior central valley, a considerable distance inland, at an elevation of 120 m. The interior of this large island supports a much denser, less xerophytic vegetation and undoubtedly has higher rainfall than does the arid coast (Felger 1966; Felger and Lowe 1976). A noteworthy gathering of A. glabrata is Wiggins 17335 (RSA) from Isla San Marcos, situated near the eastern coast of Baja Californica Sur slightly south of Santa Rosalia. All collections of this complex on the Baja California peninsula between the San Pedro Mártir in the north and La Paz in the south have pubescent culms (A. californica).

Within the Pinacate Region and Gran Desierto of northwestern Sonora, one sees a trend of more densely pubescent plants in more xeric habitats. Populations farther inland in the Gran Desierto tend to have stems more densely white-pubescent than those growing under the more equable conditions along the coast.

It seems apparent, therefore, that the distribution of pubescent and non-pubescent forms correlates with vegetational and ecological factors. Aristida glabrata occupies regions of more predictable and higher precipitation, especially summer-fall rainfall, and is replaced by A. californica in hotter, drier climates with cool season rains. Presuming the Sonoran Desert to be more recent than thornscrub, one may speculate that the origin of pubescent forms pre-dates the Sonoran Desert. Such plants may have evolved as coastal dune-

adapted plants along the great river deltas of subtropical scrub regions of northwestern Sinaloa and southwestern Sonora.

SUMMARY

The two taxa, $Aristida\ californica\$ and $A.\ glabrata$, are clearly closely related, and have the same chromosome number (2n=22). Vegetatively they are very similar, with essentially the same growth habit. Measurements of the spikelet parts show a high degree of overlap, which is complete with respect to the lemma. Nevertheless, the measurements are skewed; the longest for each character (except the lemma) was always found on plants with pubescent culms. Even though their geographical ranges are reasonably separate, and they tend to occur at different elevations, we conclude that it is more realistic to treat them as varieties of a single species. Some might prefer to designate them as subspecies, but we make no distinction between subspecies and variety when only one infraspecific level is recognized.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

THE 1989 JESSE M. GREENMAN AWARD

The 1989 Jesse M. Greenman Award has been won by Carol A. Todzia for her publication "Chloranthaceae: *Hedyosmum*," which appeared in Flora Neotropica Monographs, volume 48. This monograph is derived from a Ph.D. dissertation submitted to the University of Texas, under the direction of Dr. Beryl B. Simpson. The genus *Hedyosmum* is comprised of 40 species of predominantly montane, neotropical shrubs and trees. The comprehensive monograph, which includes four newly described species, reexamines previous treatments of the genus and presents new data on anatomy, morphology, ecology, and geography. Synopses of the taxonomic history, palynology, cytology, and uses are also provided.

This Award is named for Jesse More Greenman (1867–1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of \$500 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year.

Nominations for papers published during 1989 are now being accepted for the 22nd annual award, which will be presented in the summer of 1990. Reprints of such papers should be sent to: Greenman Award Committee, Research Division, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A. In order to be considered for the 1990 award, reprints must be received by 1 June 1990.